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ADDRESS

TO THE

PHYSIOLOGICAL SECTION

BY

W. H. GASKELL, M.D., LL.D., M.A., F.R.S.

PRESIDENT OF THE SECTION.

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WHEN I received the honour of an invitation to preside at the Physiological Section of the British Association, my thoughts naturally turned to the subject of the Presidential Address, and it seemed to me that the traditions of the British Association, as well as the fact that a Physiological Section was a comparatively new thing, both pointed to the choice of a subject of general biological interest rather than a special physiological topic; and I was the more encouraged to choose such a subject because I look upon the growing separation of physiology from morphology as a serious evil, and detrimental to both scientific subjects. I was further encouraged to do so by the thought that, after all, a large amount of the work done in physiological laboratories is anatomical—either minute anatomy or topographical anatomy, such as the tracing out of the course of nerve-fibre tracts in the central and peripheral nervous system by physiological methods. Such methods require to be supplemented by the morphological method of inquiry. If we can trace up step by step the increasing complexity of the vertebrate central nervous system; if we can unravel its complex nature, and determine the original simpler paths of its conducting fibres, and the original constitution of the special nerve centres, then it is clear that the method of comparative anatomy would be of immense assistance to the study of the physiology of the central nervous system of the higher vertebrates. So also with numbers of other physiological problems, such as, for instance, the question whether all muscular substances are supplied with inhibitory as well as motor nerves; to which is closely allied the question of the nature of the mechanism by which antagonistic muscles work harmoniously together. Such questions receive their explanation in the researches of Biedermann on the nerves of the opening and closing muscles of the claw of the crayfish, as soon as it has been shown that a genetic relationship exists between the nervous system and muscles of the crayfish and those of the vertebrate.

Take another question of great interest in the present day, viz. the function of such ductless glands as the thyroid and the pituitary glands. The explanation of such function must depend upon the original function of these glands, and cannot, therefore, be satisfactory until it has been shown by the study of comparative anatomy how these glands have arisen. The nature of the leucocytes of the blood and lymph spaces, the chemical problems involved in the assigning of cartilage into its proper group of mucin compounds, and a number of other questions of physiological chemistry, will all advance a step nearer solution as soon as we definitely know from what group of invertebrates the vertebrate has arisen.

I have therefore determined to choose as the subject of my address 'The

Origin of Vertebrates,' feeling sure that the evidence which has appealed to me as a physiologist will be of interest to the Physiological Section; while at the same time, as I have invited also the Sections of Zoology and Anthropology to be present, I request that this address may be considered as opening a discussion on the subject of the origin of vertebrates. I do not desire to speak *ex cathedra*, and to suppress discussion, but, on the contrary, I desire to have the matter threshed out to its uttermost limit, so that if I am labouring under a delusion the nature of that delusion may be clearly pointed out to me.

The central pivot on which the whole of my theory turns is the central nervous system, especially the brain region. There is the *ego* of each animal; there is the master-organ, to which all the other parts of the body are subservient. It is to my mind inconceivable to imagine any upward evolution to be associated with a degradation of the brain portion of the nervous system. The striking factor of the ascent within the vertebrate phylum from the lowest fish to man is the steady increase of the size of the central nervous system, especially of the brain region. However much other parts may suffer change or degradation, the brain remains intact, steadily increasing in power and complexity. If we turn to the invertebrate kingdom, we find the same necessary law: when the metamorphosis of an insect takes place, when the larval organs are broken up by a process of histolysis, and new ones formed, the central nervous system remains essentially intact, and the brain of the imago differs from that of the larva only in its increased growth and complexity.

A striking instance of the same necessary law is seen in the case of the transformation of the larval lamprey, or *Ammocetes*, into the adult lamprey, or *Petromyzon*; here also, by a process of histolysis, most of the organs of the head region of the animal undergo dissolution and re-formation, while the brain remains intact, increasing in size by the addition of new elements, without any sign of preliminary dissolution. On the other hand, when, as is the case in the *Tunicates*, the transformation process is accompanied with a degradation of the central nervous system, we find the adult animal so hopelessly degraded that it is impossible to imagine any upward evolution from such a type.

It is to my mind perfectly clear that, in searching among the *Invertebrata* for the immediate ancestor of the *Vertebrata*, the most important condition which such ancestor must fulfil is to possess a central nervous system, the anterior part of which is closely comparable with the brain region of the lowest vertebrate. It is also clear on every principle of evolution that such hypothetical ancestor must resemble the lowest vertebrate much more closely than any of the higher vertebrates, and therefore a complete study of the lowest true vertebrate must give the best chance of discovering the homologous parts of the vertebrate and the invertebrate. For this purpose I have chosen for study the *Ammocetes*, or larval form of the lamprey, rather than *Amphioxus* or the *Tunicates*, for several reasons.

In the first place, all the different organs and parts of the higher vertebrates can be traced directly into the corresponding parts of *Petromyzon*, and therefore of *Ammocetes*. Thus, every part of the brain and organs of special sense—all the cranial nerves, the cranial skeleton, the muscular system, &c., of the higher vertebrates can all be traced directly into the corresponding parts of the lamprey. So direct a comparison cannot be made in the case of *Amphioxus* or the *Tunicates*.

Secondly, *Petromyzon*, together with its larval form, *Ammocetes*, constitutes an ideal animal for the tracing of the vertebrate ancestry, in that in *Ammocetes* we have the most favourable condition for such investigations, viz. a prolonged larval stage, followed by a metamorphosis, and the consequent production of the imago or *Petromyzon*—a transformation which does not, as in the case of the *Tunicates*, lead to a degenerate condition, but, on the contrary, leads to an animal of a distinctly higher vertebrate type than the *Ammocetes* form. As we shall see, the *Ammocetes* is so full of invertebrate characteristics that we can compare organ for organ, structure for structure, with the corresponding parts of *Limulus* and its allies. Then comes that marvellous transformation scene during which, by a process of histolysis, almost all the invertebrate characteristics are destroyed or

changed, and there emerges a higher animal, the Petromyzon, which can now be compared organ for organ, structure for structure, with the larval form of the Amphibian; and so through the medium of these larval forms we can trace upwards without a break the evolution of the vertebrate from the ancient king-crab form. On the other hand, Amphioxus and the Tunicates are distinctly degenerate; it is easier to look upon either of them as a degenerate Ammocete than as giving a clue to the ancestor of the Ammocete. It is to my mind surprising how difficult it appears to be to get rid of preconceived opinions, for one still hears, in the assertion that Petromyzon as well as Amphioxus is degenerate, the echoes of the ancient myth that the Elasmobranchs are the lowest fishes, and the Cyclostomata their degenerated descendants.

The characteristic of the vertebrate central nervous system is its tubular character; and it is this very fact of its formation as a tube which has led to the disguising of its segmental character, and to the whole difficulty of connecting vertebrates with other groups of animals. The explanation of the tubular character of the central nervous system is the keystone to the whole of my theory of the origin of vertebrates. The explanation which I have given differs from all others, in that I consider the nervous system to be composed of two parts—an internal epithelial tube, surrounded to a greater or less extent by a segmented nervous system; and I explain the existence of these two parts by the hypothesis that the internal epithelial tube was originally the alimentary canal of an arthropod animal, such as *Limulus* or *Eurypterus*, which has become surrounded to a greater or less extent by the nervous system.

Any hypothesis which deals with the origin of one group of animals from another must satisfy three conditions:—

1. It must be in accordance with the phylogenetic history of each group. It must therefore give a consistent explanation of all the organs and tissues of the higher group which can be clearly shown not to have originated within the group itself. At the same time, the variations which have occurred on the hypothesis must be in harmony with the direction of variation in the lower group, if not actually foreshadowed in that group.

This condition may be called the Phylogenetic test.

2. The anatomical relation of parts must be the same in the two groups, not only with respect to coincidence of topographical arrangement, but also with respect to similarity of structure, and, to a large extent, also of function.

This condition may be called the Anatomical test.

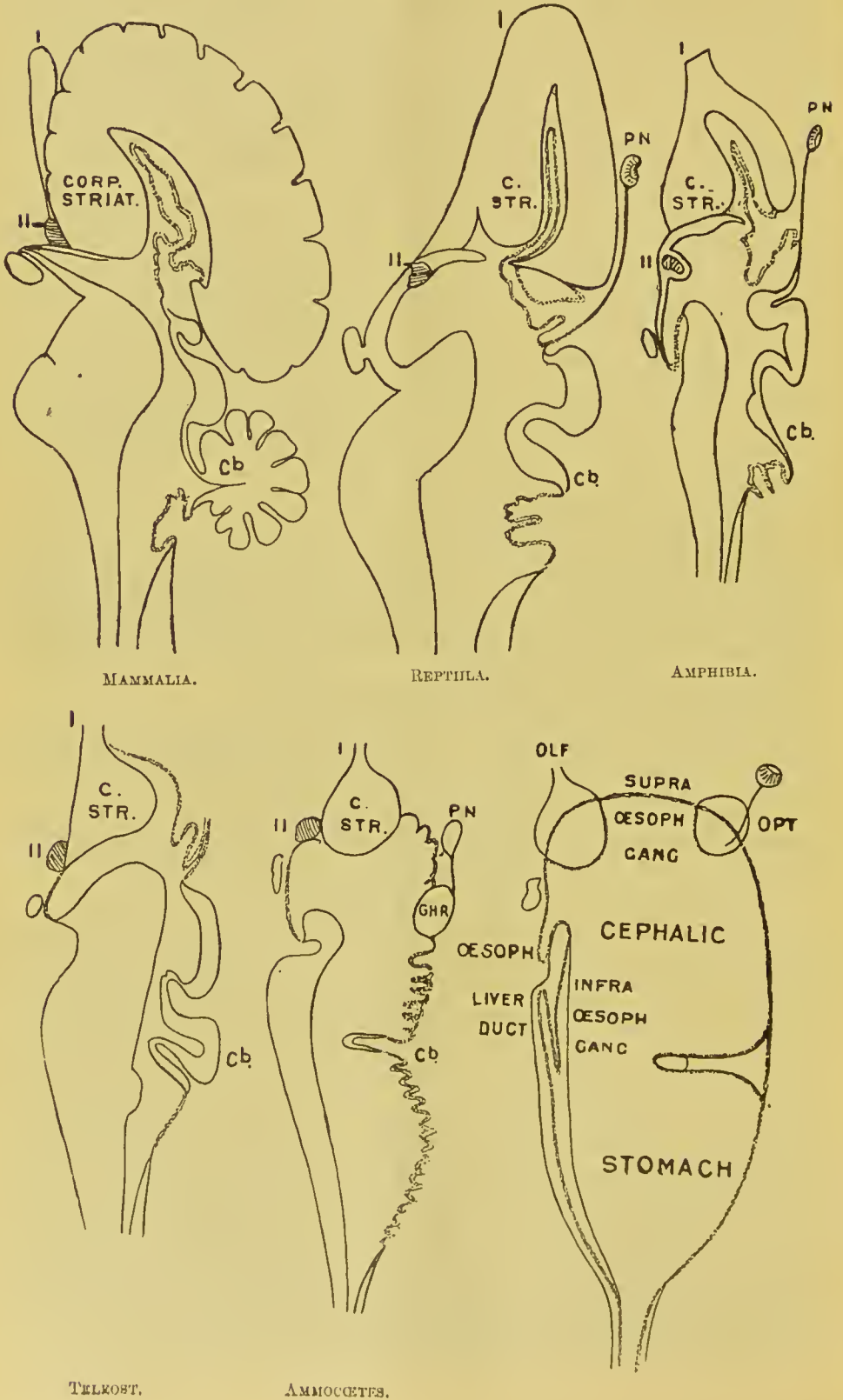
3. The peculiarities of the ontogeny or embryological development of the higher group must receive an adequate explanation by means of the hypothesis, while at the same time they must help to illustrate the truth of the hypothesis.

This condition may be called the Ontogenetic test.

I hope to convince you that all these three conditions are satisfied by my hypothesis as far as the head region of the vertebrate is concerned. I speak only of the head region at present, because that is the part which I have especially studied up to the present time, and also because it is natural and convenient to consider the cranial and spinal nerves separately; and I hope to demonstrate to you that not only the nervous system and alimentary canal of such a group of animals as the Giganostraca—*i.e.* *Limulus* and its allied forms—is to be found in the head region of Ammocetes, but also, as must logically follow, that every part of the head region of Ammocetes has its homologous part in the prosomatic and mesosomatic regions of *Limulus* and its allies. I hope to convince you that our brain is hollow because it has grown round the old cephalic stomach; that our skeleton arose from the modifications of chitinous ingrowths; that the nerves of the medulla oblongata—*i.e.* the facial, glosso-pharyngeal, and vagus nerves—arose from the mesosomatic nerves to the branchial and opercular appendages of *Limulus*, while the nerves of the hind brain are derived from the nerves of the prosomatic region of *Limulus*; that our cerebral hemispheres are but modifications of the supra-oesophageal ganglia of a scorpion, while our eyes and nose are the direct descendants of its eyes and olfactory organs.

In the first place, I will give you shortly the reasons why the central nervous

FIG. 1.—Comparison of Vertebrate Brain from Mammalia to Ammocetes. (Epithelial parts represented by dotted lines.)



system of the vertebrate must be considered as derived from the conjoined central nervous system and alimentary canal of an arthropod.

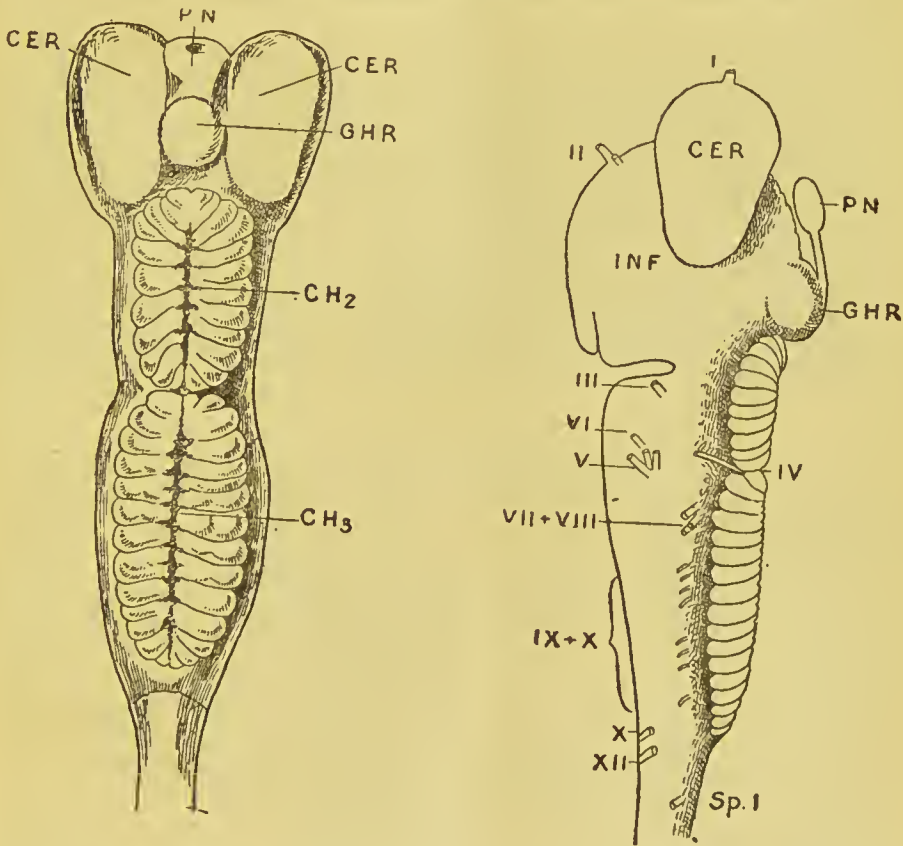
Comparison of the Central Nervous System of Ammocetes with the Conjoined Central Nervous System and Alimentary Canal of an Arthropod Animal such as Limulus.

1. *The phylogenetic test* proves that the tube of the central nervous system was originally an epithelial tube, surrounded to a certain extent by nervous material.

The anatomical test then proves that this epithelial tube corresponds in its topographical relations to the nervous material exactly with the alimentary canal of an arthropod in its relations to the central nervous system; and, further, that the topographical relations, structure, and function of the corresponding parts of this nervous material are identical in the Ammocetes and in the arthropod.

We see from these diagrams, taken from Edinger, how the greater simplicity of the brain region as we descend the vertebrate phylum is attained by the reduction

FIG. 2.—Dorsal and lateral view of the Brain of Ammocetes.



of the nervous material more and more to the ventral side of the central tube, with the result that the dorsal side becomes more and more epithelial, until at last, as is seen in Ammocetes, the roof of the epichordal portion of the brain consists entirely of fold upon fold of a simple epithelial membrane, interrupted only in one place by the crossing of the IVth nerve and commencement of the cerebellum. In the prechordal part of the brain this simple epithelial portion of the tube is continued on in the middle line as the first choroid plexus of Ahlborn, and the lamina terminalis round to the ventral side; where, again, in the infundibular region, the epithelial saccus vasculosus, which has been becoming more and more

conspicuous in the lower vertebrates, together with the median tube of the infundibulum, testifies to the withdrawal of the nervous material from this part of the brain, as well as from the dorsal region. Further, as already mentioned in my previous papers, the invasion of this epithelial tube by nervous material during the upward development of the vertebrate is beautifully shown by the commencing development of the cerebellar hemispheres in the dogfish; by the dorsal growth of nervous material to form the optic lobes in the *Petromyzon*; by the occlusion of the ventral part of the tube in the epichordal region to form the raphé, as seen in its commencement in *Ammocetes*. Finally, evidence of another kind in favour of the tubular formation being due to an original non-nervous epithelial tube is given by the frequent occurrence of cystic tumours, and also by the formation of the *sinus rhomboidalis* in birds.

The phylogenetic history of the brain of vertebrates, in fact, is in complete harmony with the theory that the tubular nervous system of the vertebrate originally consisted of two parts—viz. an epithelial tube and a nervous system outside that tube, which has grown over it more and more, and gives not only no support whatever, but is in direct opposition, to the view that the whole tube was originally nervous, and that the epithelial portions, such as the choroid plexuses and roof of the fourth ventricle, are thinned-down portions of that nerve tube. Passing now to

2. *The anatomical test*, we see immediately why this epithelial tube comes out so much more prominently in the lowest vertebrates, for, as can be seen from the diagrams, and is more fully pointed out in my previous papers,¹ every part of the central tube of the vertebrate nervous system corresponds absolutely, both in position and structure, with the corresponding part of the alimentary canal of the arthropod, and the nervous material which is arranged round this epithelial tube is identically the same in topographical position, in structure, and in function as the corresponding parts of the central nervous system of an arthropod.

Especially noteworthy is it to find that the pineal eye (PN), with its large optic ganglion, the ganglion habenulæ (GHR), falls into its right and appropriate place as the right median eye of such an animal as *Limulus* or *Eurypterus*. In the following table I will shortly group together the evidence of the anatomical test.

A. Coincidence of Topographical Position.

LIMULUS AND ITS ALLIES.	AMMOCETES AND VERTEBRATES.
<i>Alimentary Canal</i> :—	
1. Cephalic stomach.	Ventricles of the brain.
2. Straight intestine, ending in anus.	Spinal canal, ending by means of the neurenteric canal in the anus.
3. Œsophageal tube.	Median infundibular tube and saccus vasculosus.
<i>Nervous System</i> :—	
1. Supra-œsophageal ganglia.	Brain proper, or cerebral hemispheres.
2. Olfactory ganglia.	Olfactory lobe.
3. Optic ganglia of the lateral eyes.	Optic ganglia of the lateral eyes.
4. Optic ganglia of the median eyes.	Ganglia habenulæ.
5. Median eyes.	Pineal eyes.
6. Œsophageal commissures.	Crura cerebri.
7. Infra-œsophageal or prosomatic ganglia, giving origin to the prosomatic nerves.	Hind brain, giving origin to the IIIrd, IVth, and Vth cranial nerves.
8. Mesosomatic ganglia, giving origin to the mesosomatic nerves.	Medulla oblongata, giving origin to the VIIth, IXth, and Xth cranial nerves.
9. Metasomatic ganglia.	Spinal cord.

¹ Gaskell, *Journ. of Anat. and Physiol.* vol. xxiii. 1888; *Journ. of Physiol.* vol. x. 1889; *Brain*, vol. xii. 1889; *Q. J. of Micr. Sci.* 1890.

B. Coincidence of Structure and Physiological Function.

1. The simple non-glandular epithelium of the nerve tube coincides with the simple non-glandular epithelium of the alimentary canal, ciliated as it is in *Daphnia*.¹

2. The structure and function of the cerebral hemispheres, olfactory lobes, and optic ganglia closely resemble the corresponding parts of the supra-oesophageal ganglia.

3. The structure of the right pineal eye, with its nerve end-cells and rhabdites, is of the same nature as that of a median arthropod eye.

4. The structure of the right ganglion habenulæ is the same as that of the optic ganglion of the median eye.

5. The region of the hind brain, like the region of the infra-oesophageal ganglia, is concerned with the co-ordination of movements.

6. The region of the medulla oblongata, like the mesosomatic region of *Limulus* and its allies, is concerned especially with the movements of respiration.

7. The centres for the segmental cranial nerves resemble closely in their groups of motor cells and plexus substance the centres for the prosomatic and mesosomatic nerves, with their groups of motor cells and reticulated substance (Punkt-Substanz).

3. *The third test is the ontogenetic test.* The theory must be in harmony with, and be illustrated by, the embryonic development of the central nervous system. Such is the case, for we see that the nerve tube arises as a simple straight tube opening by the neurenteric canal into the anus, the anterior part of the tube, *i.e.* the cephalic stomach region, being remarkably dilated; the anterior opening of this tube, or anterior neuropore, is considered by most authors to have been situated in the infundibular region.

Next comes the formation of the cerebral vesicles, indicating embryologically the constricting growth of nervous material outside the cephalic stomach. First, the formation of two cerebral vesicles by the growth of nervous material in the position of the ganglia habenulæ, posterior commissure, and Meynert's bundle, *i.e.* the constricting influence of commissures between the optic part of the supra-oesophageal ganglia and the infra-oesophageal ganglia; then the formation of the third cerebral vesicle by the constricting influence of the IVth nerve and commencing cerebellum. Subsequently the first cerebral vesicle is divided into two parts by another nerve commissure—the anterior commissure, *i.e.* by nerve material joining the supra-oesophageal ganglia. Further, the embryological evidence shows that in the spinal cord region the nerve masses are at first most conspicuous ventrally and laterally to the original tube, such ventral masses being early connected together with the strands of the anterior commissure; ultimately, by the growth of nervous material dorsalwards, the dorsal portion of the tube is compressed to form the posterior fissure and the substantia Rolandi, the original large lumen of the old intestine being thus reduced to the small central canal of the adult nervous system. Finally, this nerve tube is formed at a remarkably early stage, just as ought to be the case if it represented an ancient alimentary canal.

The ontogenetic test appears to fail in two points:—

1. That the nerve tube of vertebrates is an epiblastic tube, whereas if it represented the old invertebrate gut it ought to be largely hypoblastic.

2. The nerve tube of vertebrates is formed from the dorsal surface of the embryo, while the central nervous system of arthropods is formed from the ventral surface.

With respect to the first objection, it might be argued, with a good deal of plausibility, that the term hypoblast is used to denote that surface which is known by its later development to form the alimentary canal; that in fact, as Heymons² has pointed out, the theory of the germinal layers is not sufficiently well established to give it any phylogenetic value. It is, however, unnecessary to discuss

Hardy and McDougall, *Proc. Camb. Philos. Soc.* vol. viii. 1893.

Heymons, *Die Embryonalentwickl. v. Dermapteren u. Orthopteren*, Jena, 1895.

this question, seeing that Heymons has shown that the whole alimentary tract in such arthropods as the earwig, cockroach, and mole cricket, is, like the nerve tube of vertebrates, formed from epiblast.

The second objection appears to me more apparent than real. The nerve layer in the vertebrate, as soon as it can be distinguished, is always found to lie ventrally to the layer of epiblast which forms the central canal. In the middle line of the body, owing to the absence of the mesoblast layer, the cells which form the notochord and those which form the central nervous system form a mass of cells which cannot be separated in the earlier stages. The nerve layer in the arthropod lies between the ventral epiblast and the gut; the nerve layer in the vertebrate lies between the so-called hypoblast (*i.e.* the ventral epiblast of the arthropod) and the neural canal (*i.e.* the old gut of the arthropod). The new ventral surface of the vertebrate in the head region is not formed until the head fold is completed. Before this time, when we watch the vertebrate embryo lying on the yolk, with its nervous system, central canal, and lateral plates of mesoblast, we are watching the embryonic representation of the original *Limulus*-like animal; then, when the lateral plates of mesoblast have grown round, and met in the middle line to assist in forming the new ventral surface, and the head fold is completed, we are watching the embryonic representation of the transformation of the *Limulus*-like animal into the scorpion-like ancestor of the vertebrates.

In the Arthropoda, the simple epithelial tube which forms the stomach and intestine is not a glandular organ, and we find that the digestive part of the alimentary tract is found in the large organ, the so-called liver. This organ, together with the generative glands, forms an enormous mass of glandular substance, which, in *Limulus*, is tightly packed round the whole of the central nervous system and alimentary canal, along the whole length of the animal (represented in fig. 4 by the dark dotted substance). The remains of this glandular mass are seen in *Ammocetes* in the peculiar so-called packing tissue around the brain and spinal cord (represented in fig. 6 by the dark dotted substance). It satisfies the three tests to the following extent:—

1. *The phylogenetic test.*—As we descend the vertebrate phylum, we find that the brain fills up the brain-case to a less and less extent, until finally in *Ammocetes* a considerable space is left between brain and brain-case, filled up with a peculiar glandular-looking material, interspersed with pigment, which is not fat tissue, and is most marked in the lowest vertebrates. The natural interpretation of this phylogenetic history is that the cranial cavity is too large for the brain in the lowest vertebrates, and is filled up with a peculiar glandular substance because that glandular substance pre-existed as a functional organ or organs, and not because it was necessary to surround the brain with packing material in order to keep it steady, owing to the unfortunate mistake having been made of forming a brain much too small for its case.

2. *The anatomical test* shows that this glandular and pigmented material is in the same position with respect to the central nervous system of *Ammocetes* as the generative and liver material with respect to the central nervous system and alimentary canal of *Limulus*.

3. *The ontogenetic test* remains to be worked out. I do not know the origin of this tissue in *Ammocetes*; the evidence has not yet been given by Kuppfer.¹ He has, however, shown that the neural ridge gives origin to a mass of mesoblastic cells, the further fate of which is not worked out. The whole story is very suggestive from the point of view of my theory, but incomprehensible on the view that the neural ridge is altogether nervous.

Finally, we ought to find in the invertebrate group in question indications of the commencement of the enclosure of the alimentary canal by the central nervous system; such is, in fact, the case. In the scorpion group a marked process of cephalisation has gone on, so that the separate ganglia, both of the prosomatic and mesosomatic region, have fused together, and fused

¹ Kuppfer, *Studien z. vergleich. Entwicklungsgesch. d. Kopfes der Kranioten*, 2. Heft, München u. Leipzig, 1894.

also with the large supra-oesophageal mass. In the middle of this large brain mass a small canal is seen closely surrounded and compressed with nervous matter, as is shown in this specimen of *Thelyphonus*; this canal is the alimentary canal. Again, Hardy, in his work on the nervous system of Crustacea, has sections through the brain of *Branchipus* which demonstrate so close an attachment between the nervous matter of the optic ganglion and the anterior diverticulum of the gut that no line of demarcation is visible between the cells of the gut wall and the cells of the optic ganglion.

For all these reasons I consider that the tubular nature of the vertebrate central nervous system is explained by my hypothesis much more satisfactorily and fully than by any other as yet put forward; it further follows that if this hypothesis enables us to homologise all the other parts of the head region of the vertebrate with similar parts in the arthropod, then it ceases to be an hypothesis, but rises to the dignity of the most probable theory of the origin of vertebrates.

Origin of Segmental Cranial Nerves.

1. *The phylogenetic test.*—It follows from the close resemblance of the brain region of the central nervous systems in the two groups of animals that the cranial nerves of the vertebrate must be homologous with the foremost nerves of such an animal as *Limulus*, and must therefore supply homologous organs. Leaving out of consideration for the present the nerves of special sense, it follows that the segmental cranial nerves must be divisible into two groups corresponding to two sets of segmental muscles, viz. a group supplying structures homologous to the appendages of *Limulus* and its allies, and a group supplying the somatic or body muscles; in other words, we must find precisely what is the most marked characteristic of the vertebrate cranial nerves, viz. that they are divisible into two sets corresponding to a double segmentation in the head region. The one set, consisting of the Vth, VIIth, IXth, and Xth nerves, supply the muscles of the branchial or visceral segments; the other set, consisting of the IIIrd, IVth, VIth, and XIIth nerves, the muscles of the somatic segments. Further, we see that the nerves supplying the branchial segments, like the nerves supplying the appendages in *Limulus*, are mixed motor and sensory, while the nerves supplying the somatic segments are all purely motor, the corresponding sensory nerves running separately as the ascending root of the fifth nerve; so also in *Limulus*, the nerves supplying the powerful body muscles arise separately from those supplying the appendages, and also are quite separate from the purely sensory or epimeral (Milne Edwards)¹ nerves which supply the surfaces of the carapace in the prosomatic and mesosomatic regions. Finally, the researches of Hardy² have shown that the motor portion of these appendage nerves, just like the nerves of the branchial segmentation in vertebrates, i.e. the motor part of the trigeminal, of the facial, of the glosso-pharyngeal, and of the vagus, arise from nerve centres or nuclei quite separate from those which give origin to the motor nerves of the somatic muscles. The phylogenetic history, then, of the cranial nerves points directly to the conclusion that the Vth, VIIth, IXth, and Xth nerves originally innervated structures of the nature of arthropod appendages.

We can, however, go further than this, for we find, as we trace downwards throughout the vertebrate kingdom the structures supplied by these nerves, that they are divisible into two well-marked groups, especially well seen in *Ammonoetes*, viz. :—

1. A posterior group, viz. the VIIth, IXth, and Xth nerves, which arise from the medulla oblongata and supply all the structures within a branchial chamber.

2. An anterior group, viz. the Vth nerves, which arise from the hind brain and supply all the structures within an oral chamber.

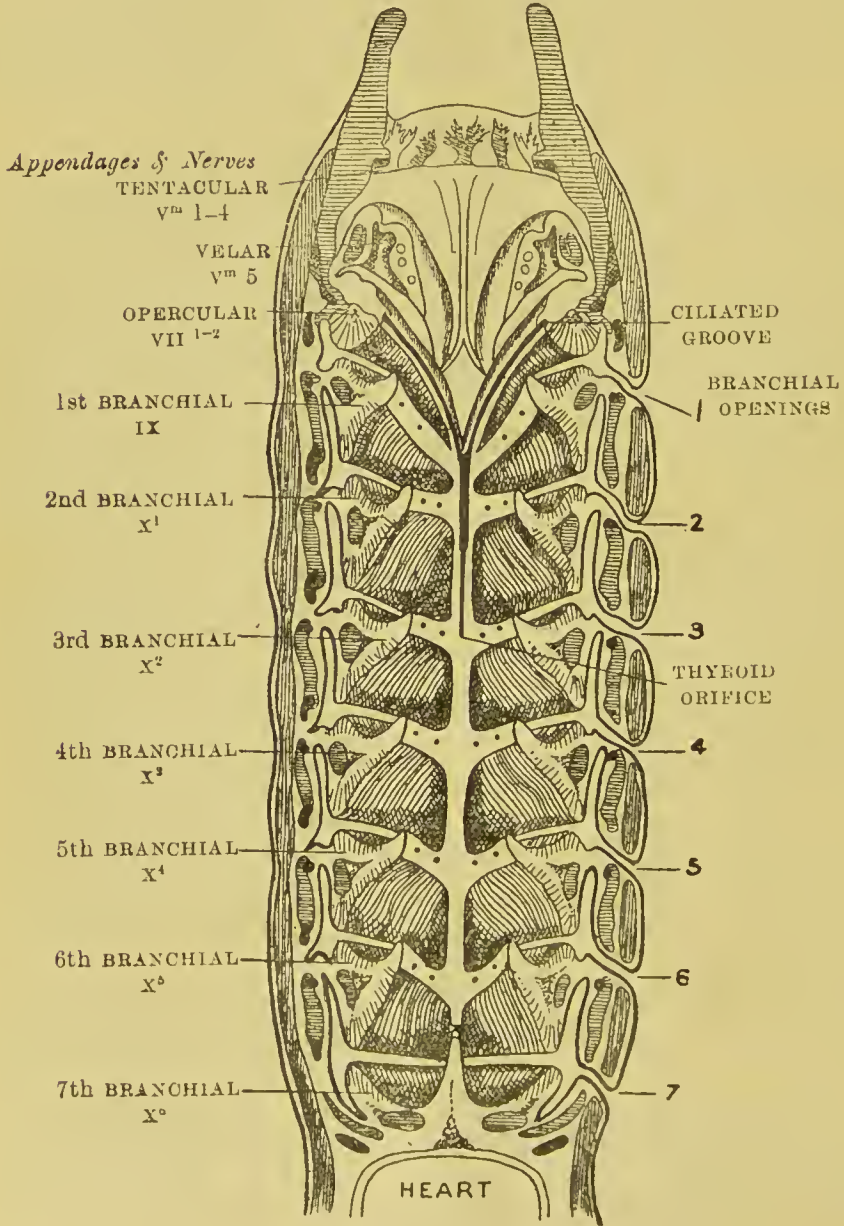
¹ Milne Edwards, 'Recherches sur l'Anatomie des *Limulus*,' *Ann. des Sc. Nat.*, 5th ser.

² Hardy, *Phil. Trans. Roy. Soc.* 1894.

The reason for this grouping is seen when we turn to *Limulus* and its allies, for we find that the body is always divided into a prosoma and mesosoma, and that the appendage nerves are divisible into two corresponding well-marked groups, viz. :—

1. A posterior or mesosomatic group, which arise from the mesosomatic ganglia and supply the operculum and branchial appendages.

FIG. 3.—Head Region of *Ammocœtes*, split longitudinally into a ventral and dorsal half. (Ventral Half.)

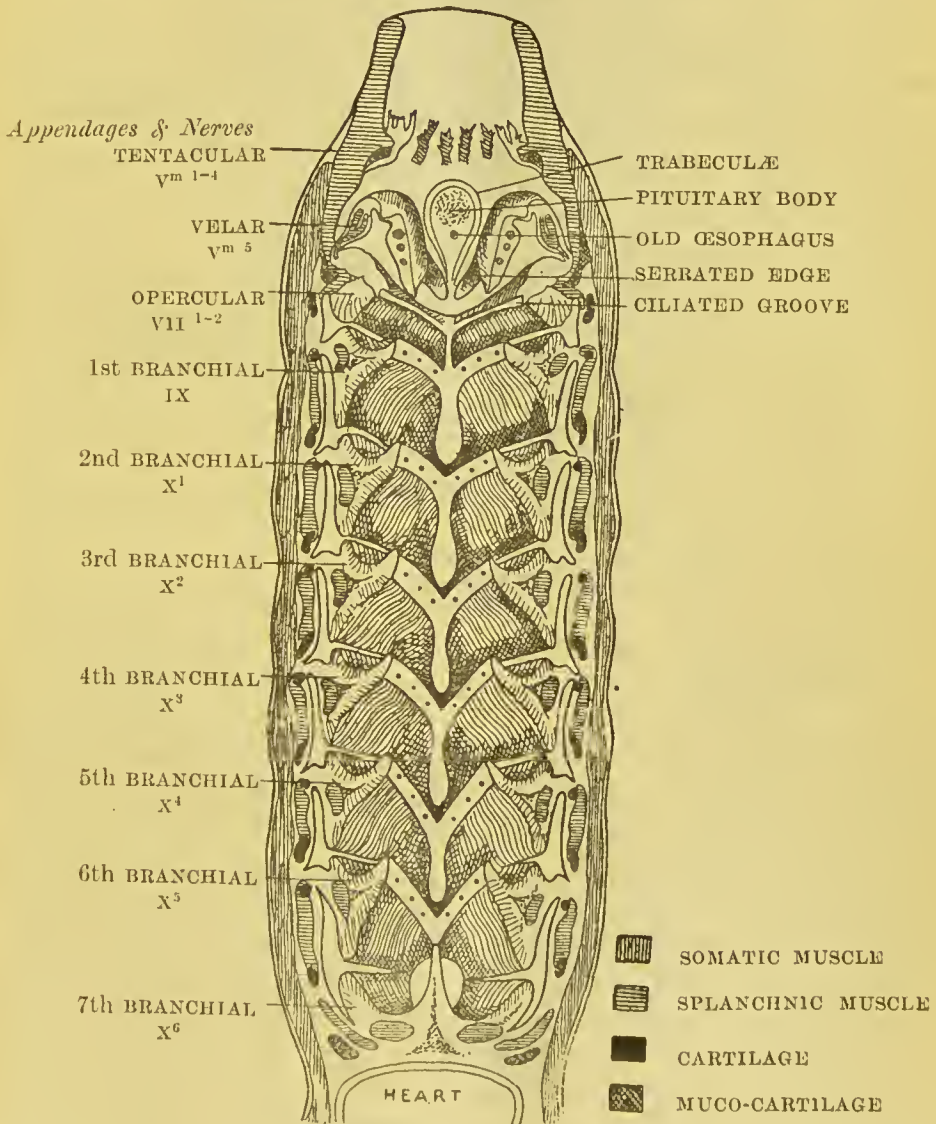


2. An anterior or prosomatic group, which arise from the prosomatic ganglia and supply the oral or locomotor appendages.

Comparison of the Branchial Appendages of Limulus, Eurypterus, &c., with the Branchial Appendages of Ammocetes. Meaning of the IXth and Xth Nerves.

We will first consider the posterior group—the VIIth, IXth, and Xth nerves—and of these I will take the IXth and Xth nerves together, and discuss the VIIth separately. These nerves are always described as supplying in the fishes the

FIG. 3.—Head Region of Ammocetes, split longitudinally into a ventral and dorsal half. (Dorsal Half.)



muscles and other tissues in the walls of a series of gill-pouches, so that the respiratory chamber is considered to consist of a series of pouches, which open on the one hand into the alimentary canal, and on the other to the exterior. Such a description is possible even as low down as *Petromyzon*, but when we pass to the *Ammocetes* we find the arrangement of the branchial chamber has become so different that it is no longer possible to describe it in terms of gill-pouches. The

FIG. 4.—Limulus. Nerves of Appendages and Cartilages.

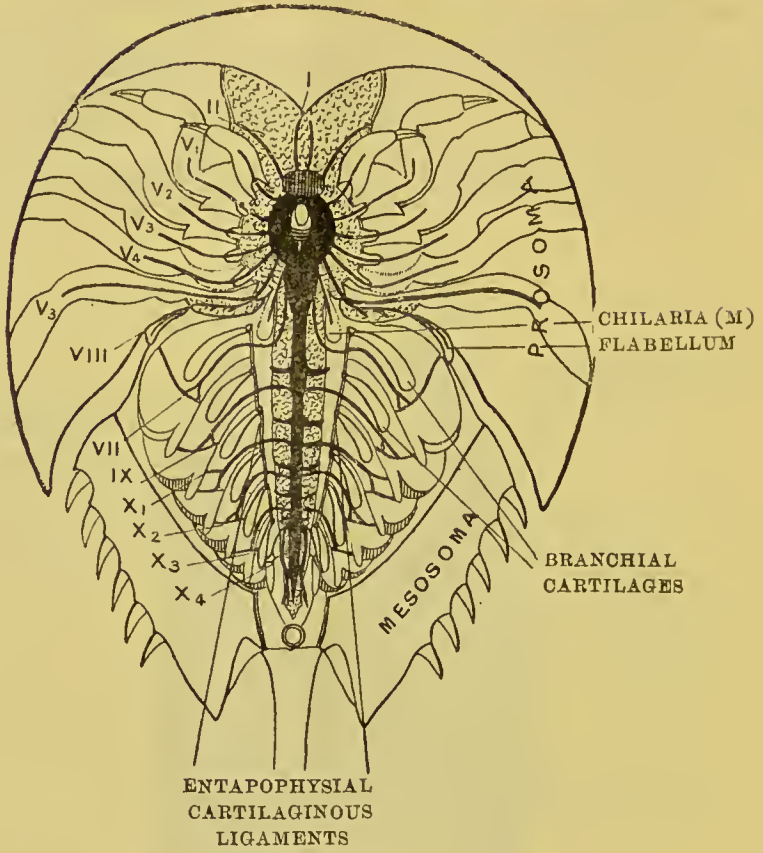


FIG. 5.—Eurypterus.

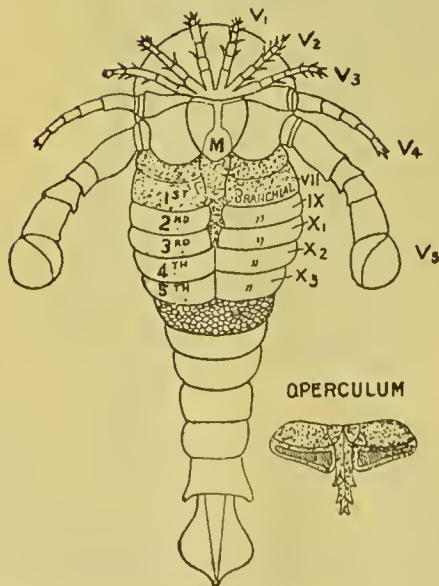
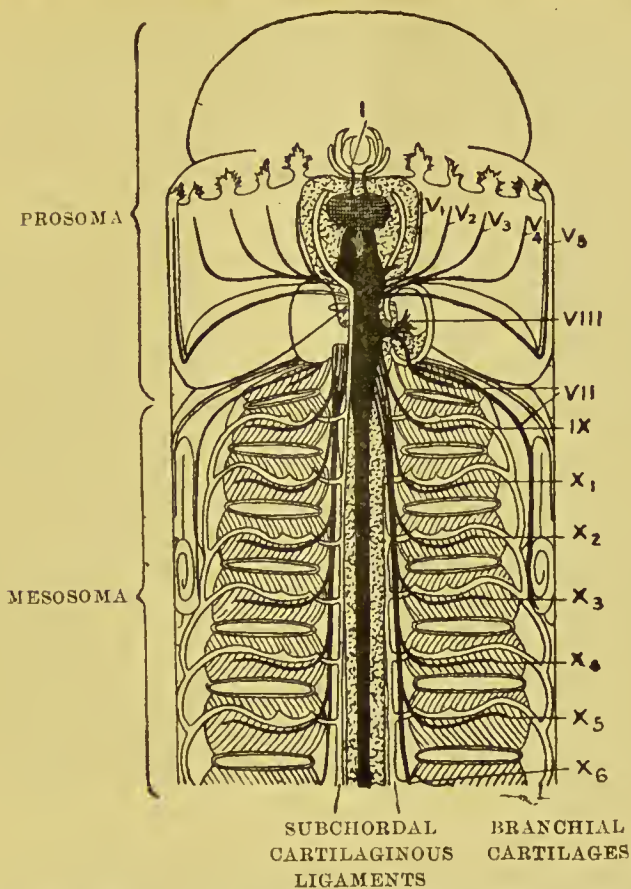


FIG. 6.—Ammocetes. Nerves of visceral segments and cartilages.



In all three Figures v_1-v_5 = Prosomatic appendages and nerves; vii = 1st mesosomatic appendage or opercular appendage and nerves; ix, x_1, \dots = remaining mesosomatic appendages and nerves; M = Chilaria in *Limulus*, metastoma in *Eurypterus*.

nature of the branchial chamber is seen in fig. 3, which demonstrates clearly that the IXth and Xth nerves supply a series of separate gill-bearing structures or appendages, which hang freely into a common respiratory chamber; each one of these appendages is moved by its own separate group of branchial muscles, and possesses an external branchial bar of cartilage, which, by its union with its fellows, contributes to form the extra-branchial basket-work so characteristic of this primitive respiratory chamber. The segmental branchial unit is clearly in this case, as Rathke originally pointed out, each one of these suspended gills, or rather gill-bearing appendages; it is absolutely unnatural, as Nestler¹ attempts to do, to take a portion of the space between two consecutive gills and call that a gill-pouch. It is, to my mind, one of the most extraordinary and confusing conceptions of the current morphology to describe an animal in terms of the spaces between organs, rather than in terms of the organs by which those spaces are formed. We might as well speak of a net as a number of holes tied together with string. Another most striking advantage is obtained by considering the segmental unit to be represented by each of these separate branchial appendages—viz. that we can continue the series in the most natural manner (as seen in fig. 3) in front of the limits of the IXth and Xth nerves, and so find a series of appendages in the oral chamber serially homologous with the branchial appendages. The uppermost of the respiratory appendages is the hyo-branchial, supplied

¹ Nestler, *Archiv f. Naturgeschichte*, 56, vol. i.

by the VIIth nerve, then, passing into the oral chamber, we find a series of non-branchial appendages, viz. the velar and tentacular appendages, supplied by branches of the Vth nerve. In fact, by simply considering the tissue between the so-called gill-pouches as the segmental unit, we no longer get lost in a maze of hypothetical gill-pouches in front of the branchial region, but find that the resemblances between the oral and branchial regions, which have led to the endless search for gill-slits and gill-pouches, really mean that the oral chamber contains appendages just as the branchial chamber, but that the former were not gill-bearing.

The study of *Ammocetes*, then, leads directly to the conclusion that the ancestor of the vertebrate possessed an oral or prosomatic chamber, which contained a series of non-branchial, tactile and masticatory appendages, which were innervated from the fused prosomatic ganglia or hind brain, and a branchial or mesosomatic chamber, which contained a series of branchial appendages which were innervated from the fused mesosomatic ganglia or medulla oblongata. These two chambers did not originally communicate with each other, for the embryological evidence shows that they are separated at first by the septum of the stomatodæum, and also that the oral chamber is formed by the forward growth of the lower lip.

The phylogenetic test on the side of *Limulus* and its congeners agrees in a remarkable manner with the conclusions derived from the study of *Ammocetes*, for we see that the variation which has occurred in the formation of *Eurypterus* from *Limulus* is exactly of the kind necessary to form the oral and branchial chambers of the *Ammocetes*. Thus, we find with respect to the mesosomatic appendages that the free, many-jointed appendages of the crustacean become converted into the plate-like appendages of *Limulus*, in which the separate joints are still visible, but insignificant in comparison with the large branchiæ-bearing lamella; then comes the in-sinking of these appendages, as described by Macleod,¹ to form the branchial lamellæ, or so-called lung-books of *Thelyphonus*, and the branchiæ of *Eurypterus*, in which all semblance of jointed and free appendages disappears and the branchiæ project into a series of chambers or gill-pouches, each pair of which in *Thelyphonus* open freely into communication. In this way we see already the commencement of the formation of a branchial chamber similar to that of *Ammocetes*.

So also with the innervation of these mesosomatic appendages, originally a series of separate mesosomatic ganglia, each of which innervates a separate appendage; then a process of cephalisation takes place, in consequence of which, in the first place, a single ganglion, the opercular ganglion, fuses with the already fused prosomatic ganglia, as is seen in the stage of *Limulus*; then, as pointed out by Lankester, in the different groups of scorpions more and more of the mesosomatic ganglia fuse together, and so we find the upward variation in this group is distinctly in the direction of the formation of the medulla oblongata coincidently with the formation of a branchial chamber.

In a precisely similar way, we find the variation which has occurred in the prosomatic appendages leads directly to the formation of the oral chamber and oral appendages of *Ammocetes*; for the original chelate and locomotor appendages of *Limulus* become converted into the tactile non-chelate appendages of *Eurypterus* (cf. figs. 4 and 5), and the small chilaria (M) of *Limulus*, according to Lankester, fuse in the middle line and grow forward to form the metastoma of *Eurypterus*, thus forming an oral chamber, into which the short tactile appendages could be withdrawn, closely similar in its formation to the oral chamber of *Ammocetes*. The prosomatic ganglia supplying these oral appendages have already, in *Limulus* (see fig. 4), been fused together to form the infra-oesophageal ganglia or hind brain.

The phylogenetic test, then, both on the side of the vertebrate and of the invertebrate, points direct to the conclusion that the peculiarities of the trigeminal and vagus groups of nerves are due to their origin from nerves supplying prosomatic and mesosomatic appendages respectively.

2. *The anatomical test* confirms and emphasises this conclusion in a most striking manner, for we find not only coincidence of topographical arrangement, as

¹ Macleod, *Archiv. de Biologie*, vol. v. 1884.

already mentioned, but also similarity of structure; thus we see that the blood in the gill lamellæ and velar appendages of *Ammocœtes* does not circulate in distinct capillaries, but, as in the arthropod appendages, in lacunar spaces, which by the subdivision of the surface of the appendage to form gill lamellæ become narrow channels; that also certain of the branchial muscles and of the muscles of the velar appendages are of the invertebrate type of so-called tubular muscles. These invertebrate muscles are not found in higher vertebrates, but only in *Ammocœtes*, and moreover disappear entirely at transformation.

Origin of the Vertebrate Cartilaginous Skeleton.

Perhaps, however, the most startling evidence in favour of the homology between the branchial segments of *Ammocœtes* and the branchial appendages of *Limulus* is found in the fact that a cartilaginous bar external to the branchiæ exists in each one of the branchial appendages of *Limulus*, to which some of the branchial muscles are attached in precisely the same way as in *Ammocœtes*. The branchial cartilages of *Limulus* (see fig. 4) spring from the entapophyses and form strong cartilaginous bars which are extra-branchial in position, just as in *Ammocœtes*, in addition to each branchial bar, a cartilaginous ligament passes from one entapophysis to another, so as to form a longitudinal or entapophysial ligament, more or less cartilaginous, which extends on each side along the length of the mesosoma. In precisely the same way the branchial bars of *Ammocœtes* are joined together along each side of the notochord by a ligamentous band of more or less continuous cartilaginous tissue, forming a subchordal or parachordal cartilaginous ligament.

Further, we see that this cartilage of *Limulus* is of a very striking structure, quite different from that of vertebrate cartilage, and that it is formed in a fibro-massive tissue which, like the matrix of the cartilage, gives a deep purple stain with thionin, thus showing the presence of some form of chondro-mucoid. This fibro-massive tissue is closely connected with the chitinogenous cells of the entapophyses.

Startling is it to find that the branchial cartilages of *Ammocœtes* possess identically the same structure as the cartilages of *Limulus*; that the branchial cartilages are formed in a fibro-massive tissue which, like the matrix of the cartilage, gives a deep purple stain with thionin, and that this fibro-massive tissue, to which Schneider¹ gives the name of muco-cartilage, or Vorknorpel, entirely disappears at transformation.

Further, according to Shipley,² the cartilaginous skeleton of the *Ammocœtes* when first formed consists simply of a series of straight branchial bars, springing from a series of cartilaginous pieces arranged bilaterally along the notochord.

The formation of the trabeculæ, of the auditory capsules, of the crossbars to form the branchial basket-work, all occur subsequently, so that exactly those parts which alone exist in *Limulus* are those parts which alone exist at an early stage in *Ammocœtes*. Another distinction is manifest between these branchial cartilages and those of the trabeculæ and auditory capsules, in that the latter do not stain in the same manner; whereas the matrix of the branchial cartilages stains red with picro-carmin, that of the trabeculæ and auditory capsules stains deep yellow, so that the junction between the trabeculæ and the first branchial bar is well marked by the transition from the one to the other kind of staining. The difference corresponds to Parker's³ soft and hard cartilage.

The new cartilages which are formed at transformation, either in places where muco-cartilage exists before or by the invasion of the fibrous tissue of the brain-case by chondroblasts, are all of the hard cartilage variety.

The phylogenetic, anatomical, and ontogenetic history of the formation of the

¹ Schneider, *Beiträge z. Anat. u. Entwicklungsgesch. der Wirbelthiere*. Berlin, 1879.

² Shipley, *Quart. Journ. of Micr. Sci.* 1887.

³ Parker, *Phil. Trans. Roy. Soc.* 1883.

vertebrate skeleton all show how the bony skeleton is formed from the cartilaginous, and how the cartilaginous skeleton can be traced back to that found in *Petromyzon*, and so to the still simpler form found in *Ammocetes*; from this, again, we can pass directly to the cartilaginous skeleton of *Limulus*, and so finally trace back the cranial skeleton of the vertebrate to its commencement in the modified chitinous ingrowths connected with the entapophyses of *Limulus*. A similar explanation of the origin of cartilage from modifications of the chitinous ingrowths of *Limulus* was suggested by Gegenbauer¹ so long ago as 1858, in consideration of the near chemical resemblances between the chitin and mucin groups of substances.

Comparison of the Thyroid and Hyo-branchial Appendage of Ammocetes with the Opercular Appendage of Eurypterus, Thelyphonus, &c. Meaning of the VIIth Nerve.

Seeing, then, how easily the IXth and Xth nerves in *Ammocetes* correspond to the mesosomatic nerves to the branchial appendages in *Limulus*, and therefore to the corresponding nerves in such an animal as *Eurypterus*, we may with confidence proceed to the consideration of the VIIth nerve, and anticipate that it will be found to innervate a mesosomatic appendage in front of the branchial appendages, and yet belonging to the branchial group; in other words, if the VIIth nerve is to fit into the scheme, it ought to innervate a structure or structures corresponding to the operculum of *Limulus* or of *Thelyphonus*, &c. Now we see in figs. 5 and 8 the nature of the operculum in *Eurypterus* and in *Thelyphonus*, *Phrynus*, &c. It is in reality composed of two parts, a median and anterior portion which bears on its under surface the external genital organs, and a posterior part which bears branchiæ; so that the operculum of these animals may be considered as a genital operculum fused to a branchial appendage, and therefore double. It is absolutely startling to find that the branchial segment immediately in front of the glosso-pharyngeal segment in *Ammocetes* (fig. 3) consists of two parts, of which the posterior, the hyo-branchial, is gill-bearing, while the anterior carries on its under surface the pseudo-branchial groove of Dohrn, which continues as a ciliated groove up to the opening of the thyroid gland.

Again, the comparison of the ventral surfaces of *Eurypterus* and *Ammocetes* (cf. fig. 5 and fig. 8) brings to light a complete coincidence of position between the median tongue of the operculum in the one animal and the median plate of muco-cartilage in the other animal, which separates in so remarkable a manner the cartilaginous basket-work of each side, and bears on its under surface the thyroid gland. Finally, Miss Alcock has shown that not only the hyo-branchial, but also the thyroid part of this segment, is innervated by the VIIth nerve; so that every argument which has forced us to the conclusion that the glosso-pharyngeal and vagus nerves are the nerves which originally supplied branchial appendages equally points to the conclusion that the facial nerve originally supplied the opercular appendage—an appendage which closed the branchial chamber in front, which consisted of two parts, a branchial and a genital, probably indicating the fusion of two segments; and that the thyroid gland belonged to the genital operculum, just as the branchiæ belonged to the branchial operculum. This interpretation of the parts supplied by the facial nerve immediately explains why Dohrn is so anxious to make a thyroid segment in front of the branchial segments, and why a controversy is still going on as to whether the facial supplies two segments or one.

What, then, is the thyroid gland? Of all the organs found in the vertebrate, with perhaps the single exception of the pineal eye, there is no one which so clearly is a relic of the invertebrate ancestor as the thyroid gland. This gland, important as it is known to be in the higher vertebrates, remains of much the same type of structure down to the fishes, and even to *Petromyzon*; suddenly, when we pass to the *Ammocetes*, to that larval condition so pregnant with invertebrate surprises, we find that the thyroid has become a large and important organ,

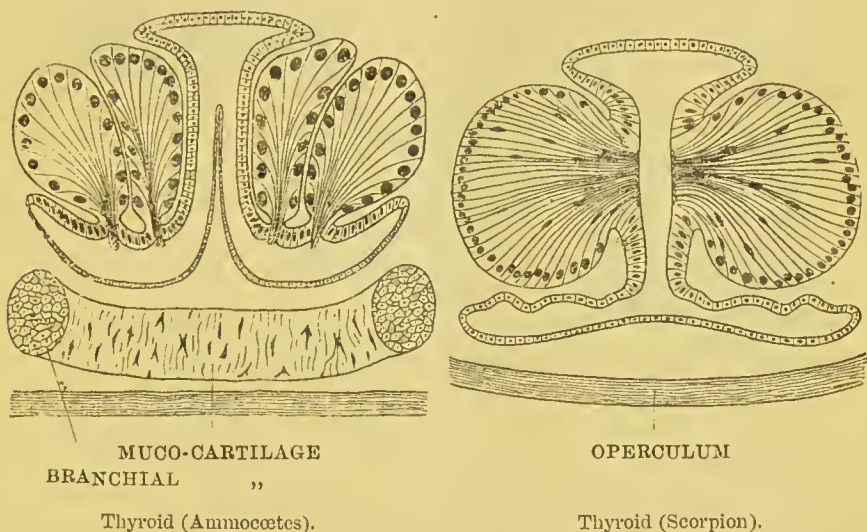
¹ Gegenbauer, 'Anat. Untersuch. eines *Limulus*,' *Abhandl. der Naturf. Gesellsch. in Halle*, 1858.

totally different in structure from the thyroid of all other vertebrates, though resembling the endostyl of the Tunicates.

The thyroid of *Ammocetes* may be described as a long tube, curled up at its posterior end, which contains in its wall, along the whole of its length, a peculiar glandular structure, confined to a small portion of its wall.

A section through this tube is given in fig. 7, and shows how this glandular structure possesses no alveoli, no ducts, but consists of a column of elongated cells arranged in a wedge-shaped manner, the apex of the wedge being in the lumen of the tube; each cell contains a spherical nucleus, situated at the very extreme

FIG. 7.

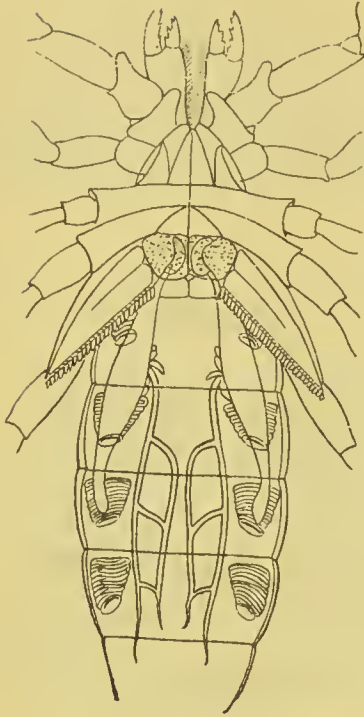


end of the cell, farthest away from the lumen of the tube. Such a structure is different from that of any other vertebrate gland. Its secretion is not in any way evident. It certainly does not secrete mucus or take part in digestion, and for a long time I was unable to find any structure which resembled it in the least degree, apart, of course, from the endostyl of the Tunicates.

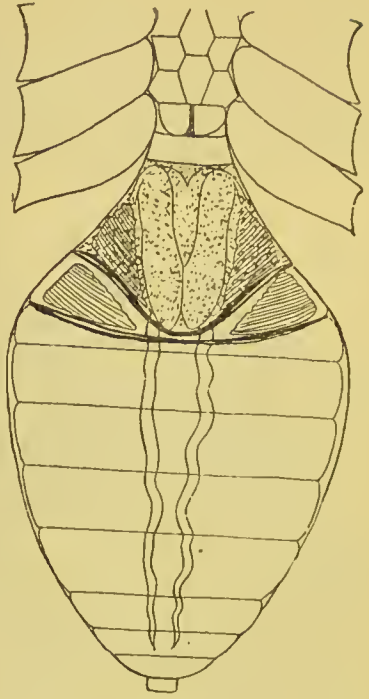
Guided, however, by the considerations already put forward, and feeling therefore convinced that in *Eurypterus* there must have been a structure resembling the thyroid gland underneath the median projection of the operculum, I proceeded to investigate the nature of the terminal genital apparatus underlying the operculum in the different members of the scorpion family, and reproduce here (fig. 8) the figures given by Blanchard¹ of the appearance of the terminal male genital organs in *Phrynus* and *Thelyphonus*. Emboldened by the striking appearance of these figures, I proceeded to cut sections through the operculum of the European scorpion, and found that that part of the genital duct which underlies the operculum, and that part only, contains within its walls a glandular structure which resembles the thyroid gland of *Ammocetes* in a remarkable degree. A section is represented in fig. 7, and we see that under the operculum in the middle line is situated a tube, the walls of which in one part on each side are thickened by the formation of a gland with long cells of the same kind as those of the thyroid; the nucleus is spherical, and situated at the farther end of the cell, and the cells are arranged in wedges, so that the extremities of each group of cells come to a point on the surface of the inner lining of the tube. This point is marked by a small round opening in the internal chitinous lining of the tube. These cells form a column along the whole length of the tube, just as in the thyroid gland, so that the chitinous lining along that column is perforated by numbers of small round

¹ Blanchard, *L'Organisation du Règne Animal*.

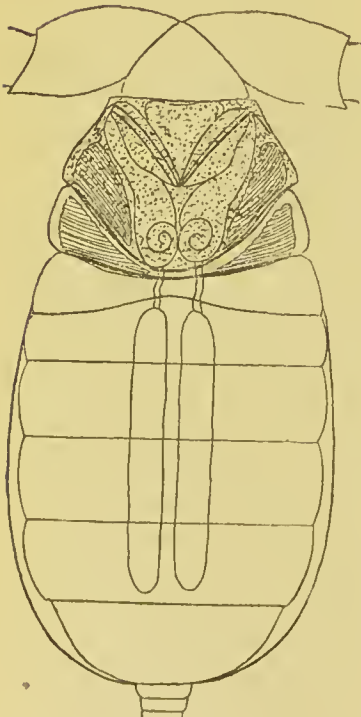
Fig. 8. Comparison of the ventral surface of the branchial region.



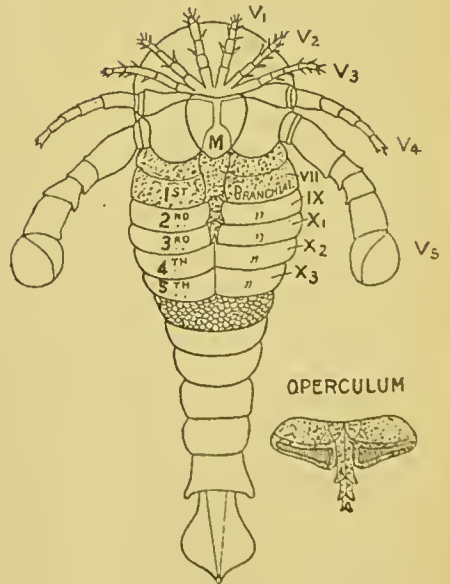
ANDROCTONUS.



PHRYXUS.



THELYPHONUS.



EURYPTERUS



AMMOCÆTES.

In all figures the opercular appendage is marked out by its dotted appearance.

holes. This glandular structure is not confined to the male scorpion, but is found also in the female, though not so well developed.

So characteristic is the structure, so different from anything else, that I have no hesitation in saying that the thyroid of Ammocœtes is the same structurally as the thyroid of the scorpion, and that, therefore, in all probability the median projection of the operculum in the old forms of scorpions, such as Eurypterus, Pterygotus, Slimonium, &c., covered a glandular tube of the same nature as the thyroid of Ammocœtes.

We see, then, that the structures innervated by the VIIth, IXth, and Xth nerves are absolutely concordant with the view that the primitive vertebrate respiratory chamber was formed from the mesosomatic appendages of such a form as Limulus by a slight modification of the method by which the respiratory apparatus of Thelyphonus and other Arachnids has been formed, according to Macleod. The anterior limit of this chamber was formed by the operculum, the basal part of which formed a septum which originally separated the branchial from the oral chamber.

*Comparison of the Oral Chamber of Ammocœtes with that of Eurypterus.
Meaning of the Vth Nerve.*

Passing now to the oral chamber—*i.e.* to the visceral structures innervated by the Vth nerve—we find, as already suggested, distinct evidence in Ammocœtes of the presence of the modified prosomatic appendages of the original Eurypterus-like form. The large velar appendage is the least modified, possessing as it does the arthropod tubular muscles, a blood system of lacunar blood-spaces, and a surface covered with a regular scale-like pattern, formed by cuticular nodosities, similar to that found on the surface of Eurypterus and other scorpions. The velar appendages show, further, that they are serially homologous with the respiratory appendages, in that they have been utilised to assist in respiration, their movements being synchronous with the respiratory movements.

The separate part of the Vth nerve which supplies the velar appendage passes within it from the dorsal to the ventral part of the animal, and then, as Miss Alcock has shown, turns abruptly forward to supply the large median tentacle. This extraordinary course leads directly to the conclusion that this median tentacle, which is in reality double, constitutes, with the velum of each side, the true velar appendages.

Again, on each side of the middle line there are in *Ammocetes* four large tentacles, each of which possesses a system of muscles, muco-cartilage, and blood-spaces, precisely similar to the median ventral tentacle already mentioned. Each of these is supplied, as Miss Alcock has shown, by a separate branch of the motor part of the Vth nerve (see fig. 6), and each branch is comparable with the branch supplying the large velar appendage.

That such tentacles are not mere sensory papillæ surrounding the mouth, but have a distinct and important morphological meaning, is shown by the fact that they are transformed in the adult *Petromyzon* into the remarkable tongue and suctorial apparatus: a modification of oral appendages into a suctorial apparatus which is abundantly common among Arthropods.

Finally, the Vth nerve innervates the visceral muscles of the lower and upper lips of *Ammocetes*. In order, then, for the story to be complete, the homologues of the lower and upper lips must also be found in the system of prosomatic appendages of forms like *Limulus* and *Eurypterus*. The lower lip, like the opercular or thyroid appendage, possesses a plate of muco-cartilage, and, as already mentioned, falls into its natural place as the metastoma of the old *Eurypterus*-like form, by the enlargement and forward growth of which the oral chamber of *Ammocetes* was formed. The meaning of the upper lip will be considered with the consideration of the old mouth tube. The comparison of the metastoma of *Eurypterus* with the lower lip of *Ammocetes* demonstrates the close resemblance between the oral chambers of *Eurypterus* and *Ammocetes*. In order to obtain the condition of affairs in *Ammocetes* from that in *Eurypterus*, it is only necessary that the metastoma should increase in size, and that the last oral appendage, the large oar-appendage, should follow the example of the other oral appendages, and be withdrawn into the oral cavity, and so form the velar appendage.

Thus we see that, just as the mesosomatic appendages of *Limulus* can be traced into the branchial and thyroid appendages of *Ammocetes* through the intermediate stage of forms similar to *Eurypterus*, so also the prosomatic appendages and chilaria of *Limulus* can be traced into the velar and tentacular appendages and lower lip of *Ammocetes* through the intermediate stage of forms similar to *Eurypterus*.

3. *Lastly comes the ontogenetic test.* The concordant interpretation of the origin of the motor part of the Vth, of the VIIth, IXth, and Xth nerves given by the anatomical and phylogenetic tests must explain and be illustrated by the facts of the development of *Ammocetes*.

We see:—

1. The oral chamber of *Ammocetes* is known in its early stage by the name of the stomatodæum, and we find, as might be anticipated, that it is completely separated at first from the branchial chamber by the septum of the stomatodæum.

2. This septum is the embryological representative of the basal part of the operculum, and demonstrates that originally the operculum separated the oral and branchial chambers.

3. Subsequently these two chambers are put into communication by the breaking through of this septum, illustrating the communication between the two chambers by the separation of the median basal parts of the operculum.

4. The velar appendages, the tentacular appendages, the lower lip, all form as out-buddings, just as the homologous locomotor appendages are formed in arthropods.

5. The branchial bars are not formed by a series of inpouchings in a tube of uniform thickness, but, as Shipley¹ has pointed out, by a series of ingrowths at

¹ *Loc. cit.*

regular intervals; in other words, the embryological history represents a series of buddings—*i.e.* appendages within the branchial chamber similar to the buddings within the oral chamber—and does not indicate the formation of gill-pouches by the thinning of an original thick tube at definite intervals.

6. The communication of the branchial chamber with the exterior by the formation of the gill-slits represents a stage in the ancestral history which is conceivable, but cannot at present be explained with the same certainty as most of the embryological facts of vertebrate development. I can only say that Strübel¹ has pointed out, and I can confirm him, that after the young *Thelyphonus* has left the egg, and is on its mother's back, before the moult which gives it the same form as the adult, the gills and gill-pouches are fully formed, but do not as yet communicate with the exterior.

7. The branchial cartilages in the *Ammocœtes* are formed distinctly before the auditory capsules and trabeculae, illustrative of the fact that they alone are formed in *Limulus*.

Comparison of the Auditory Apparatus of Ammocœtes with the Flabellum of Limulus. Meaning of the VIIIth Nerve.

The correctness of a theory is tested in two ways:—(1) It must explain all known facts; and (2) it ought to bring to light what is as yet unknown, and the more it leads to the discovery of new facts, the more certain is it that the theory is true. So far, we see that the prosomatic and mesosomatic regions of the body in *Limulus* and the scorpions are comparable with the corresponding regions of *Ammocœtes* as far as their locomotor and branchial appendages are concerned, and that, therefore, a satisfactory explanation is given of the peculiarities of the Vth, VIIth, IXth, and Xth nerves. In all vertebrates, however, there is invariably found a special nerve, the VIIIth nerve, entirely confined to the innervation of the special sense-organs of the auditory apparatus. It follows, therefore, that if my theory is true the VIIIth nerve must be found in such forms as *Limulus* and its allies, and that, therefore, a special sense-organ, probably auditory in nature, must exist between the prosomatic and mesosomatic appendages, at the very base of the last prosomatic appendage. At present we know nothing about the nature or locality of the hearing apparatus of *Limulus*. It is, therefore, all the more interesting to find that in the very position demanded by the theory, at the base of the last prosomatic appendage, is found a large hemispherical organ, to which a movable spatula-like process is attached, known by the name of the *flabellum*. This organ is confined to the base of this limb; it is undoubtedly a special sense-organ, being composed mainly of nerves, in connection with an elaborate arrangement of cells and innumerable fine hairs, which are thickly imbedded in the chitin of the upper surface of the spatula. The arrangement of these cells and hairs is somewhat similar to that of various sense-organs described by Gaubert,² and supposed to be auditory. When the animal is at rest this sensory surface projects upwards and backwards into the crack between the prosomatic and mesosomatic carapaces, so that while the eyes only permit a look-out forwards and sideways, and the whole animal is lying half buried in the sand, any vibrations in the water around can still pass through this open crevice, and so reach the sensory surface of this organ.

Finally, the most striking and complete evidence that this sense-organ of *Limulus* is homologous with the auditory capsule of *Ammocœtes* is found in the fact that in each case the nerve is accompanied into the capsule by a diverticulum of the liver and generative organs. (See dotted substance in figs. 4 and 6.) In *Limulus* the liver and generative organs, which surround the central nervous system from one end of the body to the other, do not penetrate into any of the appendages, with the single exception of the *flabellum*.

In *Ammocœtes* the peculiar glandular and pigmented tissue which surrounds

¹ Strübel, *Zool. Anzeiger*, vol. xv. 1892.

² Gaubert, *Ann. d. Sci. Nat., Zool.*, 7th ser., tome 13, 1892.

the brain and spinal cord, and has already been recognised as the remains of the liver and generative organs, does not penetrate into the velar or other appendages, but is found only in the auditory capsule, where it enters with and partly surrounds the auditory nerve.

The coincidence is so startling and unexpected as to bring conviction to my mind that in the *flabellum* of *Limulus* we are observing the origin of the vertebrate auditory apparatus; and it is, to say the least of it, suggestive that in *Galeodes* the last locomotor appendage should carry the extraordinary racquet-shaped organs which Gaubert has shown to be sense-organs of a special character, and that in the scorpion a large special sense-organ of a corresponding character, viz. the pecten, should be found which, from its innervation, as given by Patten,¹ appears to belong to the segment immediately anterior to the operculum, rather than to that immediately posterior to it.

Comparison of the Olfactory Organ of Ammocetes with the Camerostome of Thelyphonus. Meaning of the 1st Nerve. Also comparison of the Hypophysis with the Mouth-tube of Thelyphonus.

In precisely the same way as the theory has led to the discovery of a special sense-organ in *Limulus* and its allies which may well be auditory, so also it must lead to the discovery of the olfactory apparatus of the same group, for here also, just as in the case of the auditory apparatus, we are at present entirely in the dark.

The olfactory organ in such an animal as *Thelyphonus* ought to be innervated from the supra-oesophageal ganglia, and ought to be situated in the middle line, in front of the mouth. The mouth is at the anterior end in these animals, the lower lip or hypostoma (see fig. 9) being formed by the median projecting flanges of the basal joints of the two pedipalpi; above, in the middle line, is a peculiar median appendage called the camerostome. Still more dorsal we find in the median line the rostrum, with the median eyes near its extremity, and laterally on each side of the camerostome, and dorsal to it, are situated the powerful chelicerae, which are considered by some authorities to represent antennae. Of these parts the camerostome is certainly innervated from the supra-oesophageal ganglia, and upon cutting sagittal and transverse sections in a very young *Thelyphonus* we find that the surface is remarkably covered with very fine sense-hairs, arranged with great regularity and connected with a conspicuous mass of large cells. Upon making transverse sections through this region we see that the camerostome projects into the orifice of the mouth, and that its sense-epithelium forms, together with a similar epithelium on the lower lip, a closed cavity surrounded by a thick hedge of fine hairs. Here, then, in the camerostome of *Thelyphonus* is a special sense-organ which, from its position and its innervation, may well be olfactory in function, or at all events subserve the function of taste.

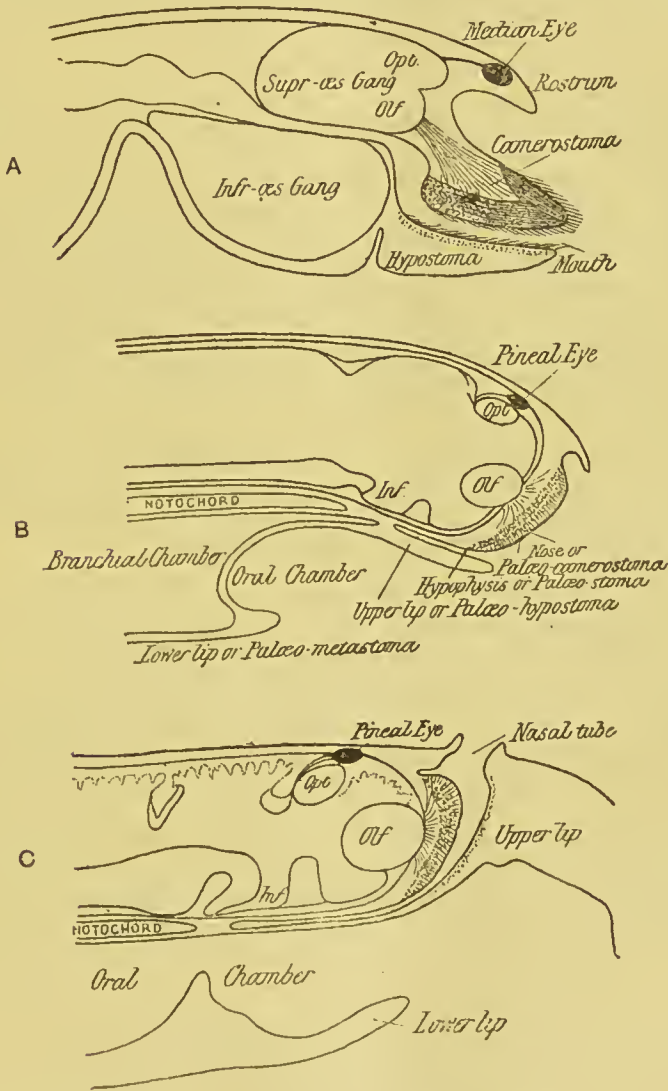
Upon comparing this organ with the olfactory organ of *Ammocetes* we see a most striking resemblance in general arrangement and structure.

Just as the mouth tube of *Thelyphonus* is formed of two parts, the pedipalp and camerostome, so, according to Kuppfer, the nasal tube of *Ammocetes* is composed of two parts, the upper lip and the olfactory protuberance. Of these two parts we see that the upper lip, or hood, like the pedipalp, is innervated by the Vth nerve, or nerve of the prosonatic appendages, while the olfactory protuberance, like the camerostome, is innervated by the 1st nerve. Kuppfer's investigations show us further (fig. 9) how the olfactory protuberance is at first free, is directed ventralwards, and lies at the opening of the hypophysial tube; how afterwards, by the forward and upward growth of the upper lip to form the hood, the nasal tube is formed, with the result that the nasal opening lies on the dorsal surface just in front of the pineal eye. Kuppfer, like Dohrn and Beard, looks upon this hypophysial tube as indicating the palaeostoma, or original mouth of the vertebrate, a view which harmonises absolutely with my theory, and receives the simplest of explanations from it, for, as you see on the screen, sections through the mouth tube

¹ Patten. *Quart. Journ. of Micr. Sci.* vol. xxxi. 1890.

of *Thelyphonus* are word for word the same as sections through the nasal tube of *Ammocoetes*; here in the one section is the projecting camerostome, here is the corresponding projection of the olfactory protuberance, here is the sense-epithelium of the upper lip or hood. Here, as fig. 9 shows, the mouth tube passes in the ventral middle line to where it turns dorsalwards into the middle of the conjoined nervous mass

FIG. 9.



A.—Median sagittal section through head of young *Thelyphonus*.
 B.— " " " " " " " " " " " " Ammocete (after Kupffer).
 C.— " " " " " " " " " " " " full-grown Ammocete (after Kupffer.)

of the supra- and infra-oesophageal ganglia. There the nasal tube ends blindly at the spot where the infundibular tube lies on the surface of the brain.

Further, the topography of corresponding parts is absolutely the same in the two animals: in the dorsal middle line the rostrum, with the two median eyes near its extremity; in the corresponding position the two pineal eyes; below this, in the middle line, the camerostome; corresponding to it in the *Ammocoetes* the olfactory

protuberance; then the modification of the median projections of the foremost ventral appendages—the pedipalpi—to form the hypostoma, in the corresponding position the upper lip or hood of *Ammocetes*, which forms the hypostoma as far as the hypophysial tube or palæostoma is concerned, but an upper lip as far as the new mouth is concerned. The muscles of this upper lip belong all to the splanchnic and not to the somatic group, and are innervated by the appropriate nerve of the prosomatic appendages, viz. the motor part of the Vth. Ventral to the pedipalpi in *Thelyphonus* there is nothing, ventral to the corresponding lip in the *Ammocetes* is the lower lip, and we have seen that, although such a structure is absent in the land scorpions of the present day, it was present in the sea scorpions of old time, was known as the metastoma, and is supposed to be a forward growth which started at the junction of the prosoma with the mesosoma. Precisely corresponding to this we see from Kuppfer that the lower lip of *Ammocetes* is a forward growth from the junction of the stomatodæum with the respiratory chamber.

We see then, so far, that the comparison of the vertebrate nervous system with the conjoined central nervous system and alimentary canal of the arthropod has led to a perfectly consistent explanation of almost all the peculiarities of the head region of *Ammocetes*. We have solved the segmentation of the skull and the mysteries of the cranial nerves, for we have found that the cranial segmentation of the vertebrate can be reduced to the segmentation of the prosomatic and mesosomatic regions of the *Limulus*, that the cranial skeleton arose from the modified internal chitinous skeleton of the *Limulus*, that the new mouth was formed by the forward growth of the metastoma, leading to the formation of an oral chamber, while the old mouth remained as the hypophysial tube, guarded by its olfactory and taste organs.

Search as we may in the prosomatic and mesosomatic regions of scorpion-like animals, there are but few points left for elucidation; among these the most important are, 1, the fate of the cœlomic cavities and coxal gland; 2, the fate of the heart; 3, the fate of the external chitinous covering.

Comparison of the Head Cavities of the Vertebrate with the Prosomatic and Mesosomatic Cœlomic Spaces of Limulus.

A recent paper by Kishinouye¹ on the development of *Limulus* enables us to compare the cœlomic cavities in the head region of a vertebrate with those of the prosomatic and mesosomatic segments of *Limulus*, and we see that the comparison is wonderfully close; for whereas each mesosomatic segment possesses a cœlomic cavity, just as each of the segments of the branchial chamber supplied by the vagus, glossopharyngeal, and facial nerves possesses a cœlomic cavity, this is not the case with the prosomatic segments. In these latter the first cœlomic cavity is a large præoral one, common to the segment of the first appendage and all the segments in front of it; the segments belonging to the second, third, and fourth appendages have no cœlomic cavities formed in them, the second cœlomic cavity belongs to the segment of the fifth appendage. Similarly in the vertebrate in the region corresponding to the prosoma there are only two head cavities recognised, viz. the 1st præoral head cavity of Balfour and V. Wijhe; and 2nd or mandibular head cavity, associated especially with the Vth nerve. According to my view the motor part of the Vth nerve represents the locomotor prosomatic appendages of *Limulus*, and we see that already in *Limulus* the three foremost of these appendages do not form cœlomic cavities.

In fact, the agreement in the formation and position of the cœlomic cavities in the head region of the vertebrate and in the prosomatic and mesosomatic regions of *Limulus* could not well be more exact; further, these cavities agree in this, that in neither case are they permanent; both in the vertebrate and in the arthropod they are supplanted by vascular spaces.

¹ Kishinouye, *Journ. of Coll. of Sci. Tokio*, vol. v. 1891.

Comparison of the Pituitary Gland with the Coxal Gland of Limulus.

In connection with the second cœlomic cavity in *Limulus* is found an ancient gland, partially degenerated according to some views, which was probably excretory in function and has been considered as homologous to the crustacean green glands. In a precisely corresponding position, and presenting a structure fairly similar to that of the coxal gland of *Limulus*, we find in *Ammocetes* and in other vertebrates the pituitary gland. How far this gland tissue is developed in connection with the mandibular head cavity I do not know, but I venture to suggest that the complete evidence of its homology with the coxal gland will be found in its developmental connection with the walls of the 2nd or mandibular head cavity.

Comparison of the Vertebrate Heart and Ventral Aorta with the Ventral Longitudinal Branchial Sinuses of Limulus and its Allies.

The heart of the vertebrate presents two striking peculiarities, which make it different from all invertebrate hearts: first, its developmental history is different; and, secondly, it is at first essentially a branchial rather than a systemic heart. The researches of Paul Mayer¹ have shown that the subintestinal vein, from which in the fishes the heart and ventral aorta arise, is in its origin double, so that in all vertebrates the heart and ventral aorta arise from two long veins which are originally situated on each side of the middle line. By the formation of the head fold these come together ventrally, coalesce into a single tube to form the subintestinal vein and heart, still remaining double as the two ventral aortæ with their branchial branches into each gill, as is well shown in the case of *Ammocetes*.

It is a striking coincidence that in *Limulus* and the Scorpions two large venous collecting sinuses are found situated in the same ventral position, for the same purpose of sending blood to the branchiæ, as already described for the vertebrate; still more striking is it to find, according to the researches of Milne Edwards and Blanchard, that these longitudinal sinuses have already begun to function as branchial hearts, for they are connected with the pericardium by a system of transparent muscles, described by Milne Edwards and named by Lankester veno-pericardiac muscles. These muscles are hollow, both near the vein and near the pericardium, so that the blood in each case fills the cavity, and, as they contract with the heart, that part of them in connection with the venous collecting sinus already functions, as pointed out by Milne Edwards and Blanchard, as a branchial heart.

By this theory, then, even the formation of the vertebrate heart is prevised in *Limulus*, and I venture to think that in *Ammocetes* we see the remnant of the old dorsal single heart of the arthropod in the form of that peculiar elongated organ composed of fattily degenerated tissue which lies between the spinal cord and the dorsal median skin.

Comparison of the Cuticular and Laminated Layers of the Skin of Ammocetes with Chitinous Layers.

The external epithelial cells of *Ammocetes* possess a remarkably thick cuticular layer. The striated appearance of this layer is due to a number of pores through which the glandular contents of the cells are poured when the surface is made to secrete. That this striated appearance is due to true porous canals, just as in chitin, and not to a series of rods, is easily seen by the inspection of sections, and also by watching the secretion through them of rose-coloured granules when the living cell is stained with methylene blue. The surface layer of this cuticular layer, according to Wolff,² resists reagents in the same manner as chitin.

¹ Mayer, *Mitth. a. d. Zool. St. zu Neapel*, vol. vii.

² Wolff, *Jen. Zeitschr.* vol. xxiii.

Internal to the epithelial cells of the skin of *Ammocetes* is a remarkable layer of tissue, generally called connective tissue. It resembles, however, histologically, in the *Ammocetes*, a section through chitin most closely; the layers are perfectly regular and parallel; cells are found in it with great sparseness, and it is not until after transformation, when it is altered and invaded by new cell elements, that it can be looked upon as at all resembling connective tissue. It resembles chitin in its reaction to hypochlorite of soda. In order to completely dissect off this laminated layer from an *Ammocetes*, all that is necessary is to place the animal in a weak solution of hypochlorite of soda, and in a short time it entirely disappears, bringing to view the muscles, branchial cartilages, pigment, front dorsal part of the central nervous system, &c., in a most striking manner. At present I am puzzled that so manifest a chitinous covering should lie internal to the epithelial cells of the surface; such a position is not, however, unknown among invertebrates, and may be accounted for in various ways.

For the sake of clearness I will sum up before you in the form of a table the corresponding parts in *Ammocetes* and in *Limulus* and its allies, as far as I have discussed them up to the present, from which you will see that there is not a single organ which is present in the prosomatic and mesosomatic regions of *Limulus* and its allies which is not found in the corresponding situation and of corresponding structure in *Ammocetes*.

Table of Coincidences between Limulus and its Allies, and between Ammocetes and Vertebrates.

LIMULUS AND ITS ALLIES.	AMMOCETES AND VERTEBRATES.
<i>Central Nervous System.</i>	
Supra-cesophageal ganglia	Cerebral hemispheres.
Optic part	Optic thalami, ganglia habenulæ, &c.
Olfactory part	Olfactory lobes.
Œsophageal commissures	Crura cerebri.
Infra-cesophageal ganglia	Epiehordal brain.
Prosomatic ganglia	Hind brain, cerebellum, post-corp. quadrig.
Mesosomatic ganglia	Medulla oblongata.
Ventral chain.	
Metasomatic ganglia	Spinal cord.
<i>Alimentary Canal.</i>	
Cephalic stomach	Ventricular cavities of brain.
Straight intestine	Central canal of spinal cord.
Terminal part	Neurenteric canal.
Œsophagus	Infundibular tube and sacculus vasculosus.
Mouth tube	Hypophysial tube, later nasal canal.
Liver	Part of subarachnoideal glandular tissue.
<i>Appendages and Appendage Nerves.</i>	
Prosomatic or locomotor appendages	Appendages of oral chamber or stomatodæum.
Foremost appendages	Upper lip and tentacles.
Last appendages	Velar appendage and median ventral tentacle.
Metastoma	Lower lip.
Nerves of prosomatic appendages	Various branches of Vth nerve.
Mesosomatic or branchial appendages	Appendages of branchial chamber.
Opercular appendages	Appendage innervated by VIth nerve.
Genital part	Thyroid gland and pseudo-branchial groove.
Branch. part	Hyobranchial.
Basal part	Septum of stomatodæum.
Branchial appendages	Branchial appendages innervated by IXth and Xth nerves.
<i>Special Sense Organs and Nerves.</i>	
Lateral eyes and optic nerves	Lateral eyes and optic nerves.
Median eyes and nerves	Pineal eyes and nerves.

Camerostoma and olfactory nerves	Olfactory organ and 1st nerve.
Flabellum and nerve	Auditory organ and VIIIth nerve.
Epimeral nerves to surface of pro- soma and mesosoma	Sensory part of Vth nerve.
<i>Internal and External Skeleton.</i>	
Internal skeleton.	
Branchial cartilages	Branchial cartilages.
Entapophysial cartilaginous ligaments	Subchordal cartilaginous ligaments.
Fibro-massive tissue (fore- runner of cartilage or 'Vorknorpel').	Muco-cartilage or 'Vorknorpel.'
External skeleton.	
Chitinous layer	Cuticular layer on-surface of body and subepithelial laminated layer.
<i>Excretory Organs and Calomic Cavities.</i>	
Coxal gland	Pituitary gland.
1st head cavity, præoral	1st head cavity, præoral.
2nd head cavity. Cavity of pro- somatic segments	2nd head cavity, mandibular.
Cavities to each mesosomatic segment	Cavities of hyoid and branchial segments.
<i>Heart and Vascular System.</i>	
Dorsal heart	Column of fatty tissue dorsal to spinal cord.
Longitudinal venous sinuses	Heart and ventral aorta.
Lacunar blood spaces of ap- pendages	Lacunar blood spaces in velar and branchial appendages.

The Possible Meaning of the Notochord.

Although we can say that every structure and organ in the prosomatic and mesosomatic regions of *Limulus*, &c., is to be found in the head region of *Ammocetes*, we cannot assert the reverse proposition, that every organ in the head region of *Ammocetes* is to be found in *Limulus*, &c., for we find a notable exception in the case of the notochord, a structure which is *par excellence* a vertebrate structure, and has in consequence given the current name to the group. Such a structure is clearly not to be found in *Limulus* and its allies; it has evidently arisen in connection with the formation of the vertebrate alimentary canal from the oral and branchial chambers, and it evidently at one time possessed a functional significance, for the lower we descend in the vertebrate scale the more conspicuous it becomes.

Unfortunately we know nothing of the condition of the notochord in the early extinct fishes, so that we are reduced to the embryological method of enquiry in our endeavours to find out the meaning of this organ. This method appears to point to the origin of the notochord from a tube connected with the alimentary canal, originally therefore an accessory digestive tube; the reasons why such a view has been put forward are, first, the origin of the notochord from hypoblast; secondly, the evidence that it is to a certain extent tubular; and thirdly, that it is an unsegmented tube extending from the oral to the anal regions of the body. Another argument, to my mind stronger than any other, is based on the principle that nature repeats herself, and if, therefore, we find the same proliferation of cells in the same place forming a series of solid notochordal rods, we may fairly argue that we are observing a series of repetitions of the same process for the same object. Now the formation of the head region of *Petromyzon* shows that at first a median proliferation of hypoblastic cells occurs to form the notochord, which then separates off from the hypoblast; later on a similar proliferation takes place to form the subnotochordal rod, which similarly separates off from the hypoblast; later still, at the time of transformation, a third median proliferation of the cells of the hypoblast takes place, to form a solid rod of cells. This solid rod then commences to hollow out at the end nearest the intestine, and the hollowing out

process extends gradually to the oral end, until a hollow tube is formed connecting the mouth with the intestine. In this way the new gut of the adult *Petromyzon* is formed from a solid median rod of cells closely resembling in its formation the original notochord.

I put it forward therefore as a suggestion, that in the ancient times when the merostomata were lords of creation and the competition was keen among these ancient arthropod forms, in which the nervous system was so arranged that increase of brain substance tended more and more to compress the food channel, and therefore to compel to the suction of liquid food instead of the mastication of solid, accessory digestive apparatuses were formed, partly in connection with the formation of the oral and respiratory chambers, and partly by means of the formation of the notochord. Of these accessory methods of digestion the former became permanent, while the latter becoming filled up with the peculiar notochordal tissue became a supporting structure, still showing by its unsegmented character its original function. That a tube formed from the external surface either as notochord or as the respiratory portion of the alimentary canal in *Ammocetes* should be capable of acting as a digestive tube is clear from the researches of Miss Alcock,¹ for she has shown that the secretion of the skin of *Ammocetes* easily digests fibrin in the presence of acid. Such a secretion, like the similar secretion of the carapace of *Daphnia* and other crustaceans, was originally for the purpose of keeping the skin clean.

The evidence which I have put before you is in agreement with the conclusion that the fore gut of the vertebrate arose gradually from a chamber formed by the lamellar branchial appendages, which functioned also as a digestive chamber. By the growth of the lower lip, or metastoma, and the modification of the basal portion of the last locomotor appendage, which basal part was inside the lower lip, into a valvular arrangement like the velum, the animal was able to close the opening into the respiratory chamber and feed as blood-sucker in the way of the rest of its kind, or, when living food was scarce, keep itself alive by the organic material taken into its respiratory chamber with the muddy water in which it lived.

The Possible Formation of the Vertebrate Spinal Region.

It remains to briefly indicate the evidence as to the formation of the rest of the alimentary canal and the spinal region of the body.

The problems connected with the formation of this region are of a different nature from those already considered in connection with the cranial region.

In the cranial region the variation that has taken place within the vertebrate group and in the course of the formation of the vertebrate is, on the whole, of the nature called by Bateson substantive, *i.e.* increase or suppression of parts, while throughout the parts remain constant in their relations to each other. It matters not whether it is frog, fish, bird, or mammal we are considering; we always find the same cranial nerves supplying the same segments. When we consider the spinal cord and its immediate junction with the cranial region, this is no longer so; here we find a repetition of similar segments, with great variation in the amount of that repetition; here we find the characteristic feature is meristic variation rather than substantive, and so indetermined is the vertebrate in this respect that even now the same species of animal varies in the number of its segments and in the arrangement of its nerves. In this part of the vertebrate body this repetition is seen not only in the central nervous system and its nerves, but also in the excretory organs, so that embryology teaches us that the vertebrate body has grown in length by a series of repetitions of similar segments formed between the head end and the tail end; such lengthening by repetition of segments has been accompanied by the elongation of the unsegmented gut, of the unsegmented notochord, and of the unsegmented neural canal.

To put it shortly, all the evidence points to and confirms the view so strongly urged by Gegenbauer, that the head region is the oldest part and the spinal

¹ Alcock, *Proc. Camb. Phil. Soc.* vol. vii. 1891.

region an afterthought, that the attempt so often made to find vertebræ and spinal nerves in the cranial region is an attempt to put the cart in front of the horse—to obtain youth from old age. We may, it seems to me, fairly argue from the sequence of events in the embryology of vertebrates that the primitive vertebrate form was chiefly composed of the head region, and that between the head and the tail was a short body region. In other words, the respiratory chamber and the cloacal region were originally close together, just as would be the case in *Limulus* if the branchial appendages formed a closed chamber. According, then, to my view, there would be no difficulty in the respiratory chamber opening originally into the cloacal region, *i.e.* the same cloacal region into which the neurenteric canal already opened. The short junction tube thus formed would naturally elongate with the elongation of the body, and, as it originally was part of the respiratory chamber, it equally naturally is innervated by the vagus nerve. This, then, is the explanation of that most extraordinary fact, *viz.* that a nerve essentially branchial should innervate the whole of the intestine except the cloacal region. Whether this is the true explanation of the formation of the mid-gut of the vertebrate cannot be tested directly, but certain corollaries ought to follow: we ought to find, on the ground that the sequence of the phylogenetic history is repeated in the embryo, that, 1, the growth in length of the embryo takes place between the cranial and sacral regions by the addition of new segments from the cranial end; 2, the formation of the fore-gut and hind-gut ought to be completed while the mid-gut is still an undifferentiated mass of yolk cells; 3. the cloacal region ought to be innervated from the sacral nerves, while the stomach, mid-gut and its appendages, liver and pancreas, ought to be innervated from the vagus.

The first proposition is a well-known embryological fact. The second proposition is also well known for all vertebrates, and is especially well exemplified in the embryological development of *Ammocetes*, according to Shipley. The third proposition is also well known, and has received valuable enlargement in the recent researches of Langley and Anderson.¹ Further, we see that in this part of the body the ancestor of the vertebrate must have had a celomic cavity the walls of which were innervated, not from the mesosomatic nerves or respiratory nerves, but from the metasomatic group of nerves; and in connection with this body cavity there must have existed a kidney apparatus, also innervated by the metasomatic nerves; with the repetition of segments by which the elongation of the animal was brought about the body cavity was elongated, and the kidney increased by the repetition of similar excretory organs. All, then, that is required in the original ancestor in order to obtain the permanent body cavity and urinary organs characteristic of the vertebrate is to postulate the presence of a permanent body cavity in connection with a single pair of urinary tubes in the metasomatic region of the body. As yet I have not worked out this part of my theory, and am therefore strongly disinclined to make any assertions on the subject. I should like, however, to point out that, according to Kishinouye,² a permanent body cavity does exist in this part of the body in spiders, known by the name of the stercoral pocket; into this celomic cavity the excretory Malpighian tubes open.

The Palæontological Evidence.

It is clear, from what has already been said, that the palæontological evidence ought to show, first, that the vertebrates appeared when the waters of the ocean were peopled with the forefathers of the Crustacea and Arachnida, and, secondly, the earliest fish-like forms ought to be characterised by the presence of a large cephalic part to which is attached an insignificant body and tail.

Such was manifestly the case, for the earliest fish-like forms appear in the midst of and succeed to the great era of strange proto-crustacean animals, when the sea swarmed with *Trilobites*, *Eurypterus*, *Slimonium*, *Limulus*, *Pterygotus*, *Ceratioceras*, and a number of other semi-crustacean, semi-arachnid

¹ Langley and Anderson, *Journ. of Physiology*, vols. xviii., xix.

² Kishinouye, *Journ. of Coll. of Sci. Tokio*, vol. iv. 1890, vol. vi. 1894.

creatures. When we examine these ancient fishes we find such forms as *Pteraspis*, *Pterichthys*, *Astrolepis*, *Bothriolepis*, *Cephalaspis*, all characterised by the enormous disproportion between the extent of the head region and that of the body. Such forms would have but small power of locomotion, and further evolution consisted in gaining greater rapidity and freedom of movements by the elongation of the abdominal and tail regions, with the result that the head region became less and less prominent, until finally the ordinary fish-like form was evolved, in which the head and gills represent the original head and branchial chamber, and the flexible body, with its lateral line nerve and intestine innervated by the vagus nerve, represents the original small tail-like body of such a form as *Pterichthys*.

Nay, more, the very form of *Pterichthys* and the nature of its two large oar-like appendages, which, according to Traquair, are hollow, like the legs of insects, suggest a form like *Eurypterus*, in which the remaining locomotor appendages had shrunk to tentacles, as in *Ammocetes*, while the large oar-like appendages still remained, coming out between the upper and lower lips and assisting locomotion. The *Ammocetes*-like forms which in all probability existed between the time of *Eurypterus* and the time of *Pterichthys* have not yet been found, owing possibly to the absence of chitin and of bone in these transition forms, unless we may count among them the recent find by Traquair of *Palæospondylus Gunnii*.

The evidence of palæontology, as far as it goes, confirms absolutely the evidence of anatomy, physiology, phylogeny, and embryology, and assists in forming a perfectly consistent and harmonious account of the origin of vertebrates, the whole evidence showing how Nature made a great mistake, how excellently she rectified it, and thereby formed the new and mighty kingdom of the *Vertebrata*.

Consideration of Rival Theories.

In conclusion I would ask, What are the alternative theories of the origin of vertebrates? It is a strange and striking fact how often, when a comparative anatomist studies a particular invertebrate group, he is sure to find the vertebrate at the end of it: it matters not whether it is the *Nemertines*, the *Capitellidæ*, *Balanoglossus*, the *Helminths*, *Annelids*, or *Echinoderms*; the ancestor of the vertebrate is bound to be in that particular group. Verily I believe the *Mollusca* alone have not yet found a champion. On the whole I imagine that two views are most prominent at the present day—(1) to derive vertebrates from a group of animals in which the alimentary canal has always been ventral to the nervous system; and (2) to derive vertebrates from the segmented group of animals, especially annelids, by the supposition that the dorsal gut of the latter has become the ventral gut of the former by reversion of surfaces. Upon this latter theory, whether it is Dohrn or van Beneden or Patten who attempts to homologise similar parts, it is highly amusing to see the hopeless confusion into which they one and all get, and the extraordinary hypotheses put forward to explain the fact that the gut no longer pierces the brain. One favourite method is to cut off the most important part of the animal, viz. his supra-cesophageal ganglia, then let the mouth open at the anterior end of the body, turn the animal over, so that the gut is now ventral, and let a new brain, with new eyes, new olfactory organs, grow forward from the infra-cesophageal ganglia. Another ingenious method is to separate the two supra-cesophageal ganglia, let the mouth tube sling round through the separated ganglia from ventral to dorsal side, then join up the ganglia and reverse the animal. The old attempts of Owen and Dohrn to pierce the dorsal part of the brain with the gut tube either in the region of the pineal eye or of the fourth ventricle have been given up as hopeless. Still the annelid theory, with its reversal of surfaces, lingers on, even though the fact of the median pineal eye is sufficient alone to show its absolute worthlessness.

Then, as to the other view, what a demand does that make upon our credulity! We are to suppose that a whole series of animals has existed on the earth, the development of which has run parallel with that of the great group of segmented animals, but throughout the group the nervous system has always been dorsal to the alimentary canal. Of this great group no trace remains, either alive at the

present day or in the record of the rocks, except one or two aberrant, doubtful forms, and the group of Tunicates and Amphioxus, both of which are to be looked upon as degenerate vertebrates, and indeed are more nearly allied to the Ammonoëtes than to any other animal. This hypothetical group does not attempt to explain any of the peculiarities of the central nervous system of vertebrates; its advocates, in the words of Lankester, regard the tubular condition of the central nervous system as in its origin a purely developmental feature, possessing no phylogenetic importance. Strange power of mimicry in nature, that a tube so formed should mimic in its terminations, in its swellings, in the whole of its topographical relations to the nervous masses surrounding it the alimentary canal of the other great group of segmented animals so closely as to enable me to put before you so large a number of coincidences.

Just imagine to yourselves what we are required to believe! We are to suppose that two groups of animals have diverged from a common stock somewhere in the region of the Cœlenterata, that each group has become segmented and elongated, but that throughout their evolution the one group has possessed a ventral mouth, with a ventral nervous system and a dorsal gut, while in the other—the hypothetical group—the mouth and gut have throughout been ventral and the nervous system dorsal. Then we are further to suppose that, without being able to trace the steps of the process, the central nervous system in the final members of this hypothetical group has taken on a tubular form of so striking a character that every part of this dorsal nerve-tube can be compared to the dorsal alimentary tube of the other great group of segmented animals. The plain, straightforward interpretation of the facts is what I have put before you, and those who oppose this interpretation and hold to the inviolability of the alimentary canal are, it seems to me, bound to give a satisfactory explanation of the vertebrate nervous system and pineal eye. The time is coming, and indeed has come, when the fetish-worship of the hypoblast will give way to the acknowledgment that the soul of every individual is to be found in the brain, and not in the stomach, and that the true principle of evolution, without which no upward progress is possible, consists in the steady upward development of the central nervous system.

